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THE INFLUENCE OF GRAVITY ON THE DIRECTION OF GROWTH OF AMANITA

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(WITH THIRTEEN FIGURES)

The following account is a record of a series of experiments carried on at the Biological Laboratory of the Brooklyn Institute at Cold Spring Harbor, under the direction of Professor D. S. JOHNSON, during the summers of 1906 and 1908. The object was to determine, if possible, the reactions of some of the common toadstools to the gravity stimulus. The main points under consideration are the promptness and accuracy of the response, the duration of the response after an efficient stimulus, the location of the zone of elongation, and its relation to the responsive zone. The conclusions here stated were drawn from observations made on about 3000 specimens, collected in the woods and replanted where conditions could be controlled. With the greatest care not more than one out of every ten planted yielded a satisfactory record. The agarics break easily, often from their own weight, when placed in a horizontal position; some shriveled instead of developing, and many were infested with the larvae of various insects, which fact was not apparent until the toadstool was near maturity.

The species used in these experiments were *Amanita phalloides* Fr. and *A. crenulata* Peck. These forms were chosen because they have long stipes, because transplanting seemed in no way to retard the normal development, and because they were very abundant. The food supply is stored in the button, so that the plant is not seriously affected by removal from the mycelium. The plants were collected from the woods just after they broke through the ground, at the stage when the pileus is beginning to break through the volva. Each was taken up carefully with some of its surrounding soil, carried to the laboratory, and there planted again in a tumbler. When it had been allowed to rest in the normal vertical position in a dark chamber for a short time, a careful drawing of each specimen was made in the following manner. The plant was placed, with the

stipe horizontal, at an accurately measured distance, before a sheet of paper firmly supported on a vertical drawing-board. In front of the toadstool and always at the same distance from it as the paper was fixed a black screen having a pinhole aperture. The drawing was made by looking through the opening and tracing the outline of the plant as it appeared against the paper. Other records were made in this way from time to time, depending upon the object of the experiment. The plant was in no way disturbed, and these records showed all changes of position in the vertical plane, and from them it was possible to measure these changes in units of angular measurements.

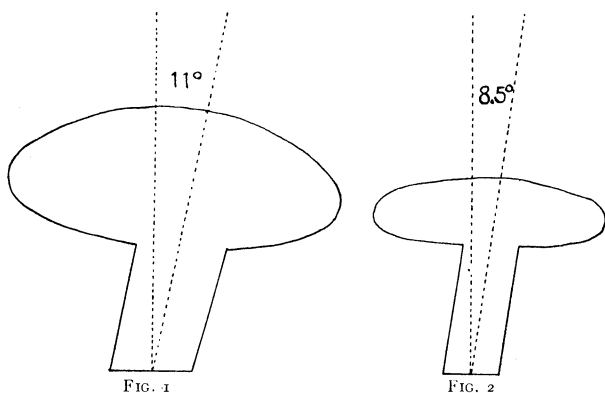


FIG. 1. *A. crenulata*, 11° from perpendicular.—FIG. 2. *A. crenulata*, $8^{\circ}5$ from perpendicular.

A few simple experiments showed that the forms used were positively heliotropic. Specimens planted in tumblers were placed in boxes which were painted black on the inside. One entire side of each box was left open and the boxes were placed in a west window with the exposed side toward the light. After standing in this position for 24 hours, the plants had bent 8° to 12° toward the light (figs. 1, 2). In fig. 1 the main axis of the toadstool is shown inclined 11° from perpendicular, and in fig. 2, $8^{\circ}5$. To avoid light stimulus, all experiments with reference to geotropism were performed within a moist dark chamber, which in turn was kept in a dark room.

After the pileus broke through the volva, it took the stipe about 24 hours to attain its full length in *A. crenulata*, and nearly 36 hours in *A. phalloides*. With a few exceptions this time element was con-

stant. This short period of development necessitated that all observations on one plant should be made within 36 hours.

In those experiments which required that the plant be held in a horizontal position, the tumbler containing the toadstool was supported firmly on a wooden block by a band of tin nailed securely to each side of the block (*figs. 3, 4*). A slender insect pin was placed in

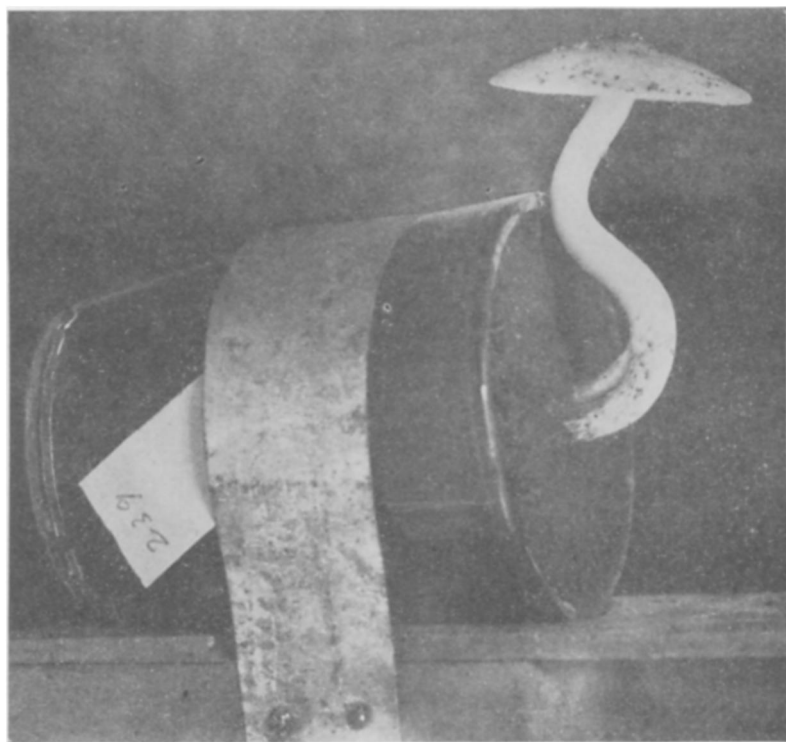


FIG. 3.—*A. phalloides*, in which supra-curvature has been neutralized.

the center of each toadstool as a continuation of the axis of the stipe (also shown in the figures). This pointer made it possible to measure the amount of curvature accurately. After being collected and planted, each specimen was left in the normal position long enough to counteract any stimulation received during its transference and then it was placed on its side in the dark chamber.

Usually the pileus does not become fully extended until after the

stipe has ceased to elongate (*fig. 5*). In 24 hours after the toadstool had reached its maximum height, the pileus expanded and its diameter increased 1.2^{cm}. In all cases where the plant was placed on its side after the stipe had reached its full length, but before the pileus

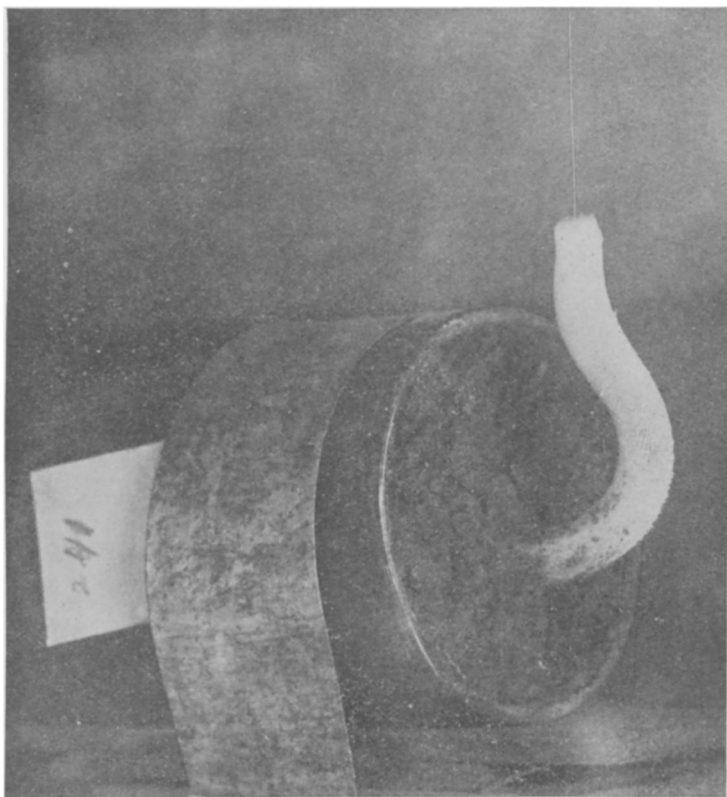


FIG. 4.—*A. phalloides*, from which the pileus, except that part directly above the stipe, has been removed.

had fully opened, the pileus continued to expand; there was, however, no upward bend in the stipe (also shown in *fig. 5*). After the stipe attains its full length there is no longer any response to gravity stimulus.

When a young plant, in which the entire stipe is still elongating, is placed on its side in the dark, the tip of the stipe begins to bend

upward after 40–60 minutes. This curvature is continued for about 24 or 36 hours, depending upon the species, until the tip of the stipe

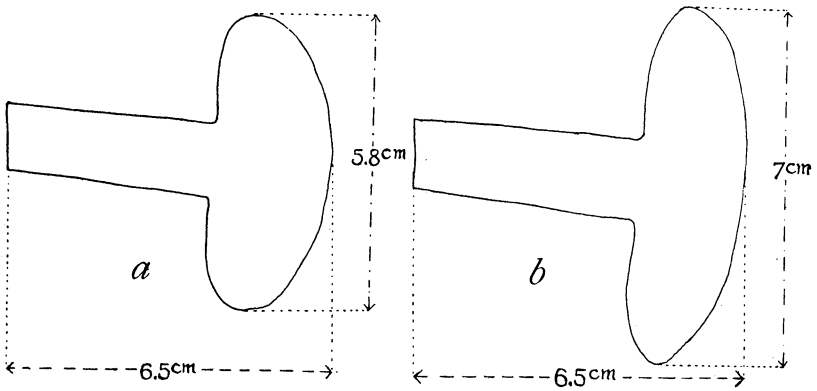


FIG. 5.—*A. crenulata*: *a*, height 6.5 cm, diameter of pileus 5.8 cm; *b*, 24 hours later, height 6.5 cm, diameter of pileus 7 cm.

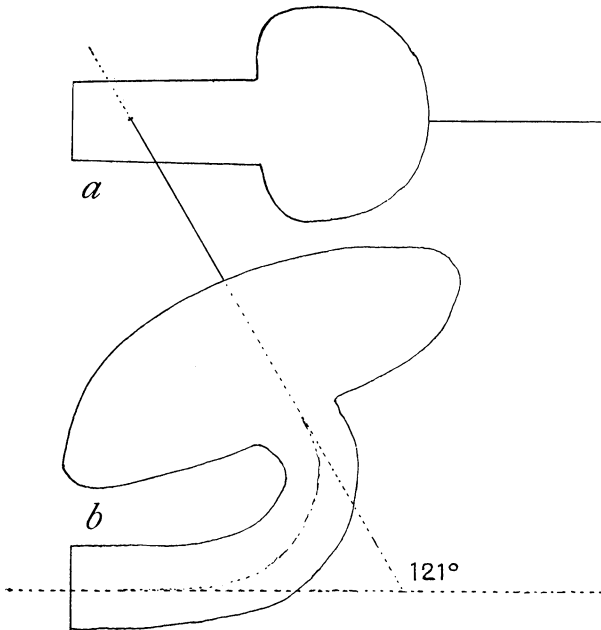


FIG. 6.—*A. crenulata*: *a*, as planted; *b*, 24 hours later, showing supra-curvature of 31°.

is carried up to and beyond the vertical position, and the original lower edge of the pileus is carried above the horizontal plane (*fig. 6*).

In experimenting with the stem of *Cephalaria procera*, one of the teasels, SACHS (1888) found that this supra-curvature was neutralized

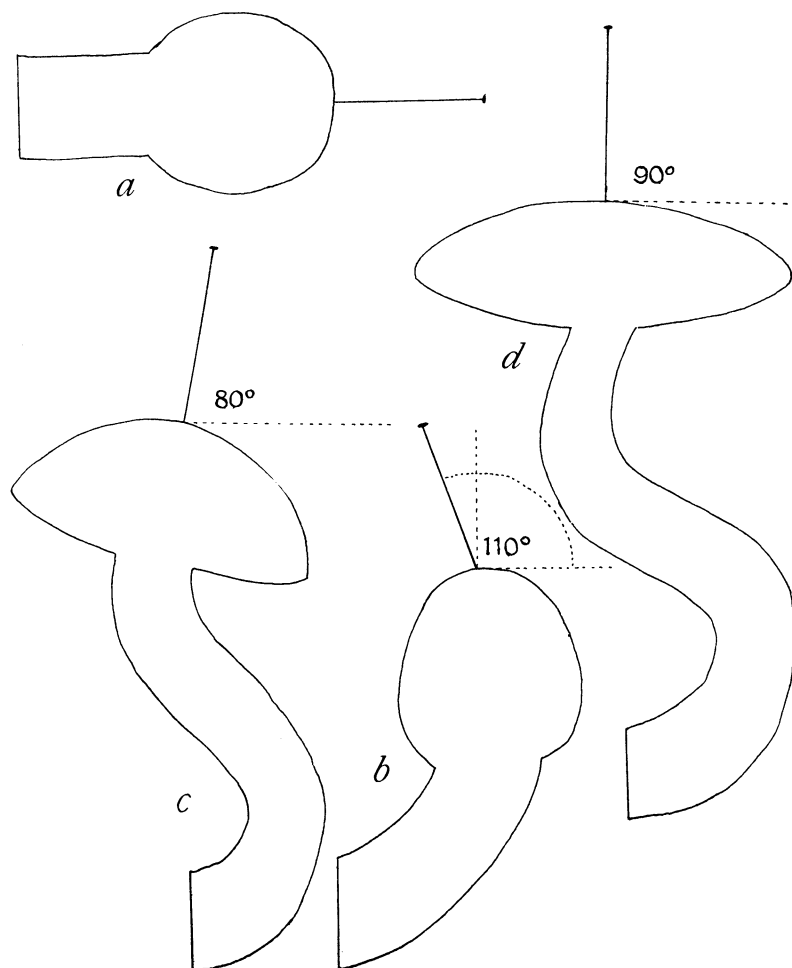


FIG. 7.—*A. phalloides*: *a*, as planted; *b*, 6 hours later, showing supra-curvature of 20°; *c*, 17 hours after planting, having returned to 10° below vertical; *d*, 30 hours after planting, tip of stipe vertical.

and the stem soon moved back to the vertical position. In the case of *A. crenulata* this supra-curvature is permanent. The probable explanation for this is that the period of elongation is so short that the reaction does not have time to take place before growth ceases.

When young specimens of *A. phalloides*, which have longer stipes and respond more quickly, were used, the tip of the stipe was carried beyond the vertical 2° to 20° , then it stopped and moved back toward and beyond the vertical 1° to 6° on the other side, and by a repetition of this process finally came to rest in the vertical position. *Fig. 7* shows a series of drawings of one specimen of *A. phalloides* in which the supra-curvature was neutralized. *Fig. 3* shows this toadstool just before it came to its final vertical position. This fluctuation only takes place if the plant is still growing when the induced response ceases.

In an attempt to locate exactly the perceptive zone, all the pileus except that part directly above and which forms a continuation of the stipe was removed in the manner shown in *fig. 8*. These plants were then allowed to develop in the dark in a horizontal position for 24 hours, and the result is shown in *fig. 8*. The stipe itself bent, but there was no curvature in that part which belonged to the pileus. This shows that the responsive zone is not situated within the pileus.

The entire pileus was then carefully removed from the tip of the stipe in many plants by a transverse cut where the gills join the stipe. Each specimen was then placed in a horizontal position in the dark and allowed to remain 24 hours. The geotropic response here was normal (*fig. 9*). The stipe, which was bent downward at first, began to bend upward slowly, then more rapidly, carrying the tip beyond the vertical. This shows that the responsive zone is situated within the stipe.

A further attempt to locate the responsive zone was made. Glass tubes were cut in pieces of different lengths and these were placed over the bases of the stipes of plants from which the pileus had been removed. This left 1-4^{mm} of the upper end of the stipe exposed beyond the end of the tube. These tubes were held firmly in a horizontal position by wire, and the plants were kept in the dark for 24 hours. In every case where elongation had not ceased, there was a decided upward curvature of the stipe beginning at the end of the glass tube (*fig. 10*). In this case the stipe was 8^{mm} long, 2^{mm} of this projecting beyond the end of the tube when the experiment was set up. After twenty-four hours the stipe projected 21^{mm} beyond the tube. It had curved upward at the end of the tube, making an

angle of 145° with the position from which it started. This shows that at least part of the responsive zone is very near the tip of the stipe. In other cases, where the stipe had nearly reached its greatest elongation, the result was the same (fig. 11). Here the stipe was

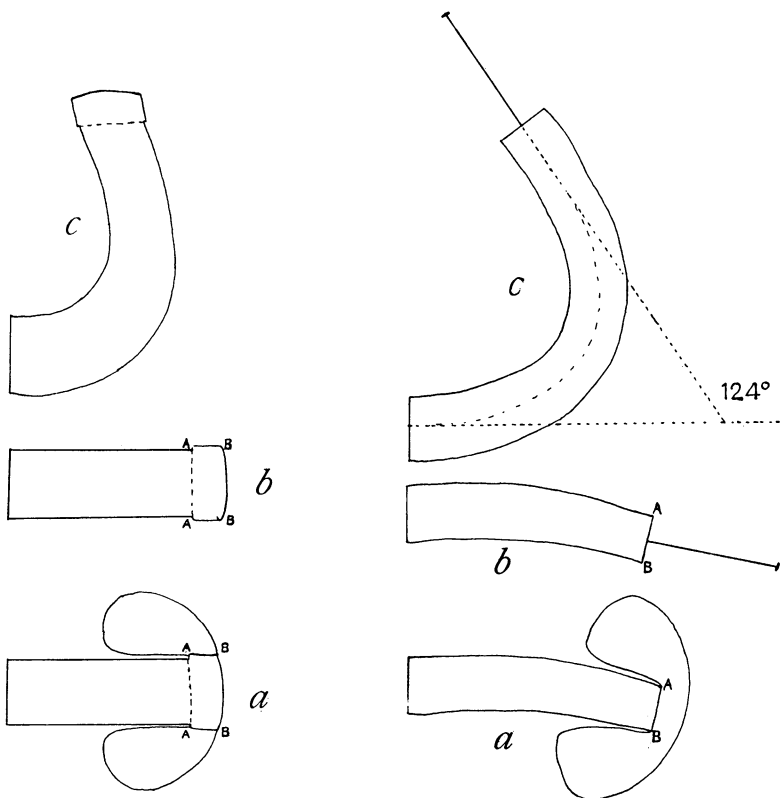


FIG. 8

FIG. 9

FIG. 8. *A. crenulata*: *a*, entire; *b*, as planted, the pileus having been removed as indicated by the lines, dotted lines show depth of pileus; *c*, 24 hours later, showing that curvature takes place in stipe, not in pileus.—FIG. 9. *A. crenulata*: *a*, entire; *b*, as planted, the pileus having been removed by transverse cut *ab*; *c*, 24 hours later, showing curvature of 124° .

56^{mm} in length, of which 1^{mm} projected beyond the end of the tube. In this case elongation continued until the stipe projected 3^{mm} , and it then showed an upward curvature of 23° . In this case the responsive zone must have been within 1^{mm} of the tip at the start.

In order to determine the distribution of the zone of elongation,

the stipes of a great many specimens in all stages of development were measured. An accurate record of the length of the stipe at the beginning and end of growth was kept. The stipe was marked off into 2^{mm} lengths with dots of waterproof India ink. It was possible,

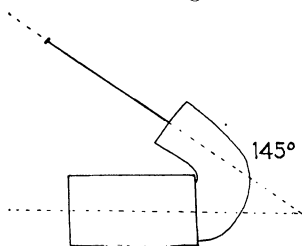


FIG. 10

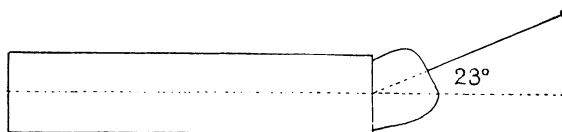


FIG. 11

FIG. 10. *A. crenulata*, 24 hours after planting; base of stipe held in glass tube; tip curved 145°.—FIG. 11. *A. crenulata*, 24 hours after planting; base of stipe held in glass tube; tip curved 23°.

when growth ceased, to tell in what region elongation had taken place and where it was most rapid. A few of these records are given below.

Number	Length of stipe at the beginning		Length of stipe at the end		Amount of elongation	Elongating portion at tip	Non-elongating region at base	Elongation in each of uppermost 2 ^{mm} spaces beginning at top	In 2d five 2 ^{mm} spaces	In 3d five 2 ^{mm} spaces	In 4th five 2 ^{mm} spaces	Comparative length of stipe at beginning	Comparative length of zone of elongation	Time
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	%	%	hours
110	7	33	26	7	0	0	7-10-5½-3½-0					21.2	100	36
216	20	50	30	20	0	0	3-3-3-3-5	4-3-2-2-2				40	100	36
218	30	68	38	30	0	0	2-2-3-3-4	4-4-3-3-2	2-2-2-1-1			44.1	100	36
157	40	72	32	40	0	0	3-4-3-3-2	2-2-1-1-1	1-1-1-1-1			55.5	100	36
104	20	34	14	20	0	0	1-2-2-2-2	1-1-1-1-1				58.8	100	36
142	30	42	12	20	10	10	2-2-2-1½-1½	1-½-½-½-½				71.4	66.6	36
148	42	52	10	20	22	22	1-2-1-1-1	1-1-1-1-1				80.7	47.6	36
138	102	104	2	8	94	94	½-½-½-½-0	1-1-1-½-½				98	7.8	36
123	36	36½	½	2	34	34	5-0-0-0-0					98.6	5.5	36

The specimens described above were grown in a horizontal position, and the measurements were taken on the lower side. Comparing the length of the stipe at the beginning and at the end of the experiment, and then comparing the length of the zone of elongation with the length of the entire stipe when the first measurement was taken, we find that elongation takes place throughout the entire length of the stipe until after it is 60 per cent. grown. From this time until

growth ceases, the zone of elongation becomes shorter and shorter, but is always just below the pileus. In the specimens used to make out the above table, the length of the mature stipe varied from 36 to 112^{mm}, and the length of the zone of elongation varied from 2 to 40^{mm}.

Record was made of the amount of elongation which had taken place in each part of the stipe beginning at the pileus. By referring to the table it can be seen that in those plants which are about one-third grown or less, the zone of most rapid elongation is in about the middle of the stipe. As growth continues, this zone moves up the stipe. In plants which are half grown or larger, the zone of most vigorous growth is the second 2^{mm} from the tip. When the zone of elongation becomes less than 4^{mm} in length, growth takes place in the upper 2^{mm} (see record for 123). The elongation within the upper 2^{mm} of the stipe is usually less than that within the second 2^{mm}, but in some cases they are equal. The amount of elongation in each 2^{mm} becomes less and less from the point of most rapid growth toward the base, until the growing region is passed.

In order to determine the time element in the geotropic response of these toadstools, plants were placed in a horizontal position in the dark and records of the amount of curvature were taken each hour. The following table gives the records of two of these specimens:

TIME	No. 51		No. 56	
	Position	Amount of change for each successive hour	Position	Amount of change for each successive hour
7:30 A. M.	0°		0°	
8:30 A. M.	-4°	-4°	5°	5°
9:30 A. M.	1°	5°	15°	10°
10:30 A. M.	4°	3°	23°	8°
11:30 A. M.	8°	4°	32°	9°
12:30 P. M.	11°	3°	42°	10°
1:30 P. M.	15°	4°	52°	10°
2:30 P. M.	19°	4°	62°	10°
3:30 P. M.	22°	3°	72°	10°
4:30 P. M.	24°	2°	82°	10°
5:30 P. M.	26°	2°	88°	6°
6:30 P. M.	28°	2°	92°	4°
7:30 P. M.	30°	2°	95°	3°
8:30 P. M.	32°	2°	97°	2°
9:30 P. M.	32°	0°	98°	1°
7:30 A. M.	32°	0°	98°	0°

In about two-thirds of all the plants placed in a horizontal position in these experiments, there was a bending downward of 1° to 6° during the first hour, before there was any observable upward curvature. This may be partly due to wilting caused by transplanting. In general this downward tendency was less in the younger specimens where the stipe is shorter, and it was less where the pileus had been removed. These facts seem to indicate that it might be the physical effect of a new lateral strain rather than a response to a new stimulus. For this reason in many cases the pileus was removed, as is shown in *fig. 4*. No. 51 shows this bend downward in the first hour, followed by 1° more than complete recovery in the second hour. For the next six hours the rate of curvature fluctuated from 3° to 4° per hour; this was followed by a steady rate of 2° per hour for five hours; then the pileus came to rest at an angle of 32° from horizontal. In No. 56 the response during the first hour was slight; during the second it was greatly accelerated; this was followed by a period of depression which lasted for one or two hours; from this time on for the next five or six hours the reaction was constant and rapid, then more slow. After the vertical line was passed, the curvature took place more and more slowly until, in the case cited here, it came to rest at an angle of 98° from its original position. Nine hours later, or 24 hours from the start, it remained in the same position and there had been no increase in length. There was no neutralization of the 8° of supra-curvature.

In order to determine the exposure period, that is, the length of time which the plant must be stimulated in order that reaction may follow, several plants were kept in a fixed horizontal position for 15 minutes and were then rotated on a clinostat about the horizontal axis for 24 hours. The plants gave a decided reaction to geotropic stimulation for this length of time. There was an upward curvature of the stipe varying from 15° to 30° from its position during exposure to the stimulus. Four records of plants of *A. phalloides*, stimulated by being in a horizontal position for 5 minutes and rotated on a clinostat for 24 hours, showed an upward curvature of 7° , 10° , 10° , and 15° , respectively. Eight records of plants of both *A. phalloides* and *A. crenulata* stimulated for one minute all show an upward curvature of either 6° or 7° . In one case of stimulation for 5 minutes,

in three cases of stimulation for one minute, and in all cases (ten records) where the specimens were in a horizontal position only 30 or 15 seconds, there was no direct upward curvature. Instead, the stipe had made a definite spiral curvature in the same direction as that in which the clinostat moved. Clinostats which rotated in opposite directions were used and the spiral always followed the direction of the clinostat (*fig. 12*).

To find the latent period, the pileus was carefully removed that curvature might not be retarded by the weight which would cause a strain in an unusual place and the plants were placed in a horizontal position. Records were made every 10 minutes. In young, vigorously growing specimens, there was an upward curvature observable in 40 minutes. In other specimens which were nearer maturity, the period was longer, in some cases being 60 minutes.

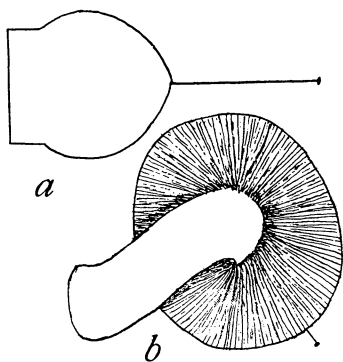


FIG. 12

FIG. 12. *A. phalloides*: *a*, as placed on clinostat; *b*, 24 hours later, showing special curvature of stipe.—FIG. 13. *A. phalloides*, showing amount of curvature for each 10 minutes for 80 minutes.



FIG. 13

No records which showed the downward bend were considered in this experiment. The diagram (*fig. 13*) shows the rate of curvature in a typical specimen.

SUMMARY

When young and vigorously growing toadstools were placed with the stipe in the horizontal position, the stipe of each toadstool bent and carried the pileus up to or beyond the horizontal position. This supra-curvature when it occurred was neutralized if growth did not cease too soon.

The responsive zone is situated near the tip of the stipe, not within the pileus.

The stipe elongates throughout its entire length, until it is more

than half grown. The zone of most rapid elongation is always just below the pileus and becomes shorter and shorter until growth ceases.

When placed in the horizontal position, the tip of the stipe curved upward very slowly at first, then more rapidly, until it passed the vertical position, after which the curvature took place more slowly until it came to rest. If growth were still vigorous, the tip of the stipe again passed the vertical, rested on the other side, and finally assumed the ordinary position.

The amount of time which a toadstool must be stimulated in order that reaction may follow is less than a minute. How much less was not satisfactorily determined, probably because the clinostats used rotated too slowly.

The latent period varied from 40 to 60 minutes, the younger specimens responding more quickly.

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